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Cestoda from Lake Fishes in Wisconsin: The Ecology and Pathology of *Proteocephalus ambloplitis* Plerocercoids in Their Fish Intermediate Hosts

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ABSTRACT: Seventeen species of fish in 5 families were infected with parenteric plerocercoids of *Proteocephalus ambloplitis* in 2 southeastern Wisconsin eutrophic lakes. The records from *Carpiodes cyprinus* and *Moxostoma erythrurum* are new. Prevalence and intensity were considerably higher in the land-locked Silver Lake compared to the river-connected Tichigan Lake. Plerocercoids were present in various hosts during all seasons but were most prevalent and numerous during the spring; subsequent decreases of plerocercoids in bass were attributed to parenteric recruitment into bass gut. Recruitment via the nonparenteric route is believed to have a significant role in the *P. ambloplitis* suprapopulation cycling in Wisconsin, particularly when fish other than bass, e.g., *Amia calva,* are involved as definitive hosts. Accordingly, recruitment does not have to occur only once a year, and the critical May temperatures of 7–12°C would not be required under all circumstances. Parenteric plerocercoids were localized mostly in the intestinal mesenteries during the spring but shifted to the gonads, liver, and spleen in summer and autumn. Some pathological observations are noted including the unilateral hypertrophy of infected ovaries in centrarchid fishes.

KEY WORDS: *Proteocephalus ambloplitis,* plerocercoids, Wisconsin fishes, ecology.

The bass tapeworm, *Proteocephalus ambloplitis* (Leidy, 1887), has been reported throughout the United States and southern Canada by many authors. Cooper (1915) and Bangham (1927) provided some early observations on its life history, which was more completely worked out by Hunter (1927, 1928) and Hunter and Hunter (1929). It was not until the work of Fischer and Freeman (1969, 1973) in Ontario that the actual life history of *P. ambloplitis* in bass became available. Findings by these latter authors corrected some of the earlier misconceptions and clarified for the first time the actual contribution of parenteric plerocercoids to the development of enteric *P. ambloplitis* in bass. Freeman (1973) classified 4 types of *P. ambloplitis* plerocercoids: (1) plerocercoid I in the copepod, (2) initial plerocercoid II in the body cavity of *Micropterus* or other fish genera, (3) middle plerocercoid II only in the body cavity of bass, and (4) terminal plerocercoid II only in the gut of bass either by entry from parenteral sites in the same fish (termed parenteric recruitment) or cannibalism. Anatomical aspects of these plerocercoid types are currently being examined and evaluated by our laboratory. Other reports that, at least partially, dealt with the role of plerocercoids include those of Esch et al. (1975) in Michigan and Eure (1976) in South Carolina. None of the above reports, however, examined the seasonal ecology of parenteric plerocercoids in their fish intermediate hosts, the subject matter of this report. New aspects of plerocercoid pathology are also included.

Materials and Methods

The fishes examined were from Silver Lake (Kenosha County), a 188-ha eutrophic land-locked lake, and from Tichigan Lake (Racine County), a 458-ha lake in an advanced state of eutrophication on the Fox River (a tributary of the Mississippi River). Seasonal collections were made from both lakes during the spring (April), summer (June, July, and early August), and autumn (late October and November) between 1977 and 1979 and from Silver Lake during the summer of 1976. One thousand eight hundred twelve fishes representing 32 species from 10 families (Amiidae, 1 species; Catostomidae, 7; Centrarchidae, 9; Cyprinidae, 2; Esocidae, 2; Ictaluridae, 4; Lepisosteidae, 1; Percidae, 2; Salmonidae, 2; Serranidae, 2) were captured by electroshocking from both lakes. An additional 1,543 fishes representing 29 species from 11 families (Amiidae, 1; Catostomidae, 3; Centrarchidae, 6; Cyprinidae, 5; Cyprinodontidae, 2; Esocidae, 2; Gasterosteidae, 1; Ictaluridae, 4; Percidae, 3; Serranidae, 1; Umbridae, 1) were captured primarily using seines or minnow traps in a channel draining the swampy western area of Tichigan Lake during 1978 and 1979.

Fish were systematically dissected shortly after capture. Plerocercoids were individually dissected out of visceral organs, i.e., liver, spleen, gonads. Fish infected with uncounted (few to > 1,000) young encysted plerocercoids in their intestinal walls are included in the prevalence but not the mean values (Table 1). Specimens were processed as in Amin (1986a) and mounted whole for microscopical examination. Paraffin-embedded histopathologic sections were cut 10 μm thick and stained in hematoxylin and eosin.

Results and Discussion

Plerocercoids of *P. ambloplitis* were found in 17 species of fishes from 5 families. Centrarchidae included the largest number of species (7) with the heaviest infection (Table 1). The infections recorded from *Carpiodes cyprinus* and *Moxostoma erythrurum* (Catostomidae) are new host records. Fish species negative for parenteric plerocercoid infections in both lakes as well as in Tichigan Lake canal were *Amia calva* (55 fishes) (Amiidae); *Carpiodes carpio* (3), *Catostomus commersoni* (75), *Moxostoma anisurum* (4), *M. carinatum* (3) (Catostomidae); *Chaenobryttus gulosus* (1), *Pomoxis annularis* (19) (Centrarchidae); *Cyprinus carpio* (82), *Notropis cornutus* (107), *N. umbratilis* (33), *Pimephalus* sp. (765) (Cyprinidae); *Fundulus notatus* (19), *F. notti* (6) (Cyprinodontidae); *Esox americanus* (5), *E. lucius* (44) (Esocidae); *Culaea inconstans* (182) (Gasterosteidae); *Noturus gyrinus* (2) (Ictaluridae); *Etheostoma nigrum* (123) (Percidae); *Oncorhynchus mykiss* (1), *Salmo trutta* (1) (Salmonidae); *Roccus chrysops* (23), *R. mississippiensis* (1) (Serranidae); and *Umbra limi* (86) (Umbridae).

Lake distribution

Prevalence and intensity of infection were considerably higher in the land-locked Silver Lake than in the larger river-connected Tichigan Lake in all seasons. This pattern corresponds with that of enteric *P. ambloplitis* infecting both species of bass and *Amia calva* during the same seasons (Amin and Cowen, 1990). The populations of some fish parasites, e.g., caryophyllaeid cestodes, neoechinorhynchid acanthocephalans (Amin, 1986a, b) appear to become larger and better established in closed lake systems, e.g., Silver Lake, than in open lakes having continuous exchange with a river system, e.g., Tichigan Lake. Whether this pattern is related to the distribution and abundance or diapause patterns of the crustacean intermediate hosts or factors relating to the fish intermediate hosts is not known. Differences in lake turnover rates may be important.

Seasonal distribution

Parenteric plerocercoids were present during all seasons investigated but were clearly most prevalent and numerous during the spring and decreased during the summer and further during the autumn. The presence of parenteric plerocercoids in their fish hosts throughout the year was also reported in Ontario (Fischer and Freeman, 1969), Michigan (Esch et al., 1975), South Carolina (Eure, 1976), Oklahoma (McDaniel and Bailey, 1974), and Arkansas (Cloutman, 1975). Maximum seasonal means in South Carolina were observed during April and May (Eure, 1976). More than 50% of the Wisconsin parenteric plerocercoids from Silver Lake (287/510) during the spring were from *M. salmoides* (Table 1). The loss of parenteric middle plerocercoid II individuals to enteric penetration in bass is likely responsible for the subsequent decreases in observed parenteral infection. Such parenteral entry was documented mostly during May in bass from Ontario (Fischer and Freeman, 1969) and Michigan (Esch et al., 1975), when critical temperatures of 7–12°C were reached. The post-spring decline in parenteric plerocercoid numbers may have also been influenced by seasonal changes in fish host size, assuming that larger fish will ingest greater volumes of the same food items eaten by smaller fish. Of the 3 most important host species in Silver Lake, in terms of level of infection and sample size (Table 1), largemouth bass showed a decline in size (total length in cm) from a mean of 36.4 (range, 21–48) in the spring to 29.2 (17–46) and 23.7 (12–42) in summer and autumn, respectively. Bluegill size was stable at 15.7 (8–21), 14.3 (11–17), and 15.6 (10–21), respectively; and walleye summer decline in size disappeared by the autumn with 37.1 (28–53), 27.7 (16–33), and 38.9 (25–54), respectively. Size composition of plerocercoids was not a good indicator of infection periodicity; it was more closely associated with the body cavity organs they infected. The recovery of well-developed plerocercoids that were smaller than less-developed ones was not uncommon.

Recruitment (parenteric entry of middle plerocercoid II into bass gut) may also occur parenterally once a year in Wisconsin during the spring (Table 2; Amin and Cowen, 1990) once the critical temperature of 7–12°C is reached, as has been suggested both by Fischer and Freeman (1969) in Ontario and by Esch et al. (1975) in Michigan (up from 4°C), and by Eure (1976) in South Carolina (down from 26°C). Less-developed plerocercoids not so recruited would remain in extraintestinal sites of bass, as well as other fish species, as a future source of adults. For further discussion, see Seasonal site selection and Kennedy (1983). Bailey's (1984) observation of increased intensity of *P. ambloplitis* plerocercoids with increasing age of *Lepomis macrochi-*

Table 1. Seasonal distribution of parenteric plerocercoids of *Proteocephalus amblopliti*s from fishes in Silver and Tichigan lakes proper, 1976–1979.*

Fish species	Silver Lake			Tichigan Lake		
	Spring (Apr)	Summer (late Jun–early Aug)	Autumn (late Oct; Nov)	Spring (Apr)	Summer (late Jun–early Aug)	Autumn (late Oct; Nov)
Catostomidae						
Carpiodes cyprinus	–†	–	–	–	1/13 (7), 0, 0 (1)	0/6
Erimyzon sucetta	2/27 (7), 3, 0.1 (0)	0/25	2/42 (5), 7, 0.2 (0)	–	–	–
Moxostoma erythrurum	–	–	–	–	0/4	2/4 (50), 0, 0 (2)
Centrarchidae						
Ambloplites rupestris	3/4 (75), 3, 0.8 (3)	4/8 (50), 40, 5.0 (1)	4/13 (31), 1, 0.1 (4)	2/2 (100), 0, 0 (2)	–	–
Lepomis cyanellus	0/5	5/13 (38), 0, 0 (5)	–	2/7 (29), 0, 0 (2)	0/5	1/6 (17), 0, 0 (1)
Lepomis gibbosus	5/6 (83), 18, 3.0 (0)	0/9	1/1 (100), 0, 0 (1)	0/15	0/32	0/13
Lepomis macrochirus	34/62 (55), 66, 1.1 (0)	29/98 (30), 36, 0.4 (0)	50/141 (35), 50, 0.3 (0)	0/51	0/74	1/87 (1), 1, 0.01 (0)
Micropterus dolomieui	2/2 (100), 3, 1.5 (0)	1/2 (50), 25, 12.5 (0)	–	1/6 (17), 0, 0 (1)	0/10	0/2
Micropterus salmoides	18/28 (64), 287, 10.3 (0)	19/38 (50), 378, 9.9 (0)	2/6 (33), 5, 0.8 (0)	1/2 (50), 0, 0 (1)	5/19 (26), 24, 1.3 (0)	5/23 (22), 7, 0.3 (0)
Pomoxis nigromaculatus	5/25 (20), 70, 2.8 (0)	2/4 (50), 8, 2.0 (0)	2/18 (11), 2, 0.1 (0)	0/70	0/33	2/59 (3), 0, 0 (2)
Ictaluridae‡						
Ictalurus melas	0/1	0/1	1/1 (100), 1, 1.0 (0)	0/6	–	0/2
Ictalurus natalis	1/2 (50), 6, 3.0 (0)	1/2 (50), 6, 3.0 (0)	–	0/7	0/1	–
Ictalurus punctatus	–	–	–	1/17 (6), 3, 0.2 (0)	1/12 (8), 0, 0 (1)	0/6
Lepisosteidae						
Lepisosteus osseus	3/3 (100), 15, 5.0 (0)	5/11 (45), 14, 1.3 (0)	–	–	0/9	–
Percidae						
Perca flavescens	0/4	2/37 (5), 4, 0.1 (0)	2/26 (8), 3, 0.1 (0)	0/57	0/3	0/17
Stizostedion vitreum	9/21 (43), 39, 1.9 (0)	3/10 (30), 4, 0.4 (0)	5/23 (22), 5, 0.2 (0)	0/4	0/20	0/28
Total	82/188 (44), 510, 2.7 (3)	71/258 (27), 516, 2.0 (6)	69/271 (25), 74, 0.3 (5)	7/244 (3), 3, 0.01 (6)	7/235 (3), 24, 0.1 (2)	11/253 (4), 8, 0.03 (5)

* Number of fish infected/number examined (% prevalence), number of plerocercoids recovered, mean plerocercoids per examined fish (number of fish infected with encysted plerocercoids in intestinal wall, calculated in prevalence but not in mean intensity because of the undetermined number of cysts).

† No fish examined.

‡ The gut wall of one *Ictalurus nebulosus* from Tichigan Lake (misc. coll.) was studded with many encysted plerocercoids (Figs. 3, 4).

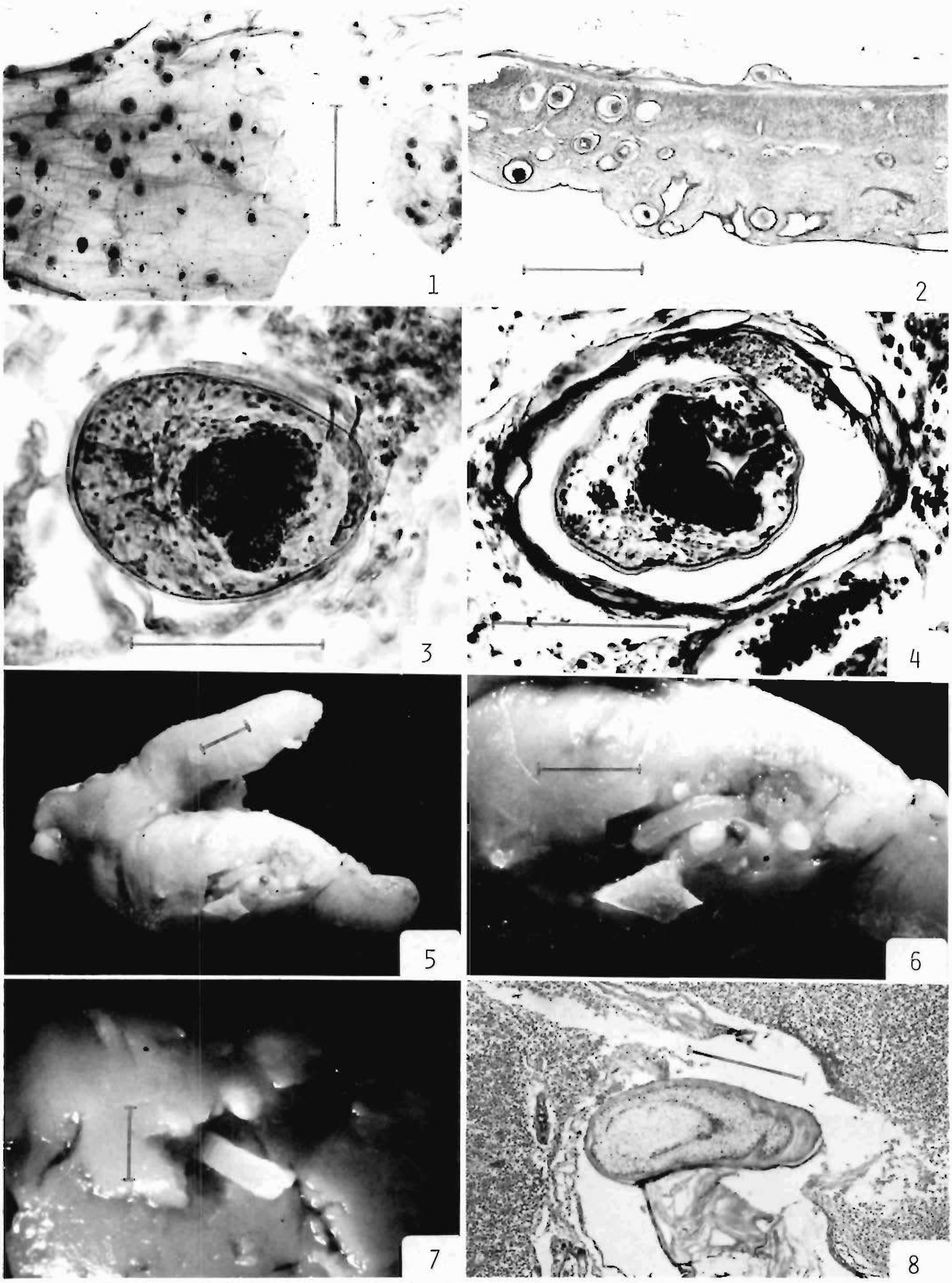
Table 2. Parenteric distribution of *Proteocephalus ambloplitis* plerocercoids in fishes from Silver and Tichigan lakes (combined) during spring, summer, and autumn, 1976–1979.

	Total number of worms (*N*) and proportion (%) recovered from											
	Spring (Apr)				Summer (late Jun–early Aug)				Autumn (late Oct, Nov)			
Fish species	*N*	% in M*	% in Go†	% in L/S‡	*N*	% in M	% in Go	% in L/S	*N*	% in M	% in Go	% in L/S
Catostomidae												
Erimyzon sucetta	3	—	100	—	0	—	—	—	7	—	100	—
Centrarchidae												
Ambloplites rupestris	3	—	100	—	40	88	—	12	1	100	—	—
Lepomis gibbosus	18	67	—	33	0	—	—	—	0	—	—	—
Lepomis macrochirus	66	35	18	47	36	3	11	86	51	31	—	69
Micropterus dolomieui	3	100	—	—	25	80	—	20	0	—	—	—
Micropterus salmoides	287	57	39	4	402	6	72	22	12	—	58	42
Pomoxis nigromaculatus	70	98	2	—	8	100	—	—	2	100	—	—
Ictaluridae												
Ictalurus melas	0	—	—	—	0	—	—	—	1	—	—	100
Ictalurus natalis	6	100	—	—	6	—	—	100	0	—	—	—
Ictalurus punctatus	3	100	—	—	0	—	—	—	0	—	—	—
Lepisosteidae												
Lepisosteus osseus	15	—	—	100	14	—	—	100	0	—	—	—
Percidae												
Perca flavescens	0	—	—	—	4	—	—	100	3	—	—	100
Stizostedion vitreum	39	31	2	67	4	100	—	—	5	100	—	—
Total	513	57	25	18	536	16	55	29	82	30	18	52

* Primarily from the mesenteries but occasionally including non-site-specific forms in the body cavity.
† From the gonads, almost exclusively the ovaries.
‡ Mostly from the liver but occasionally the spleen.

rus was interpreted as reflecting plerocercoid longevity. This pattern of infection is interpreted as a means of dispersal in time augmenting the common method of dispersal in space (via host movement) characteristic of most cestodes. Such brevipatent one-time seasonal breeders as *P. ambloplitis* in bass with a short adult life span and long plerocercoid life are semelparous. Of course, Bailey's (1984) observations may also express an increased probability of exposure due to greater food intake by larger fish. The extended residence of some cestodes, e.g., certain pseudophyllideans, in the crustacean intermediate host may also provide an alternate explanation of *P. ambloplitis* dispersal in time.

Although Fischer and Freeman (1969), Esch et al. (1975), and Eure (1976) discussed recruitment only in the context of parenteric entry of plerocercoids into the bass gut, the potential importance of cannibalism was not recognized. Only Fischer and Freeman (1973) pointed to the potential ecological importance of transport fish hosts as a link between copepods and bass. Findings from Wisconsin suggest a considerably greater significance of this pathway in the cycling of *P. ambloplitis* in its fish hosts. For example, parenteric plerocercoids infected a wide diversity of fish hosts (Table 1) throughout the year but with seasonality, not limited to bass, that was similar to that of enteric stages (above; Amin and Cowen, 1990) and although temperatures of 7–12°C may be critical for parenteric recruitment into the intestines of some bass during the spring, no critical temperatures for recruitment via cannibalism are indicated from the Wisconsin data. Actually the term "cannibalism" is misleading because it implies that only *Micropterus* can become the definitive host of enteric *P. ambloplitis* by feeding on other *Micropterus* infected with parenteric middle plerocercoid II. In several lakes in Wisconsin, *A. calva* harbors even larger populations of adult *P. ambloplitis* than bass (Amin and Cowen, 1990) which can be acquired by feeding on plerocercoid-infected bass. *Amia calva* was not infected with *P. ambloplitis* plerocercoids in Wisconsin. The role of other fish species as an intermediate link between copepods and bass (or bowfin) cannot be overemphasized.



Figures 1–8. Histopathology of ***Proteocephalus ambloplitis*** plerocercoids in various organs of some Wisconsin fish intermediate hosts. 1. A section of ***Lepomis gibbosus*** intestinal wall studded with encysted larvae. 2. A longitudinal section of ***Ambloplites rupestris*** gut wall showing migrating cysts. 3. A differentiating encysted plerocercoid in the gut wall of ***Ictalurus nebulosus***; note the vacuolated host tissue. 4. A later stage of encysted plerocercoid in the gut wall of ***I. nebulosus***. 5. Unilateral enlargement in infected ***L. macrochirus*** ovary. 6. Enlargement of infected ovary in Figure 5; the dark eggs are dead. 7. Intrahepatic invasion by grown plerocercoid(s). 8. A histopathologic section from same liver in Figure 7 showing part of the plerocercoid and host tissue vacuolation and leukocytosis. Figures 5–7: dark field. Scale bars in Figures 1, 2, 8 = 1.0 mm; 3, 4 = 100 μm; 5–7 = 5.0 mm.

Probably, recruitment into the adult *P. amblo-plitis* suprapopulation as a whole does not have to occur once a year and is not limited to bass in the spring but may extend to other definitive hosts, e.g., *A. calva*, where the parenteric pathway is not applicable. The role of other definitive hosts, e.g., *Roccus chrysops* and *R. mississippiensis* (Arnold et al., 1968; McReynolds and Webster, 1980) remains unknown. In the *A. calva* case, "critical" May temperatures of 7–12°C would not be required unless this temperature is necessary for transformation of middle to terminal plerocercoid II regardless of the mode of entry into the definitive host gut. The findings of Amin and Cowen (1990) that recruitment into *A. calva* extends through the summer and autumn months do not support that possibility. Copepod dynamics, e.g., timing and duration of diapause, may be important in establishing variability in recruitment cycles.

Seasonal site selection

Information on the seasonal distribution of parenteric plerocercoids in various body cavity sites is available from 13 species of fish (Table 2). Plerocercoids were mostly localized in intestinal mesenteric tissue (57%) during the spring but shifted to the gonads (55%) during the summer and the liver and spleen (52%) during the autumn. This was particularly true in *M. salmoides* that had the largest sample. In bass, the shift was primarily to gonadal sites and probably represents parenteric (intestinal mesentery) loss of middle plerocercoid II individuals to the gut. Whether gonadal, splenic, and hepatic forms become available to recruitment into the intestine at a later date or become lost except for possible transfer to a predator fish is not known. In *Lepomis macrochirus,* a considerable and increasing presence in the liver was noted. The decrease in intestinal mesentery sites between spring and summer (Table 2) is attributed to the migration of plerocercoid I across the bluegill intestinal wall prior to transformation to initial plerocercoid II in extraintestinal sites. The above data (Tables 1, 2) provide qualified field support for the Fischer and Freeman (1969) initial explanation of the migration and recruitment of the plerocercoid stage(s) of *P. ambloplitis.*

Pathology

The mass migration of encysted plerocercoid I individuals was observed in a few centrarchid fishes, particularly *Ambloplites rupestris* during all seasons (Table 1). Whole intestines were seen studded with hundreds of such cysts (Figs. 1, 2). Some of these cysts were clearly double walled, with the outer wall appearing to be of host origin (Figs. 3, 4)—a new observation. This cyst stage directly follows the ingestion of infected copepods by these fish intermediate hosts. The mode of plerocercoid penetration through the intestinal wall of these fish while enclosed within a cyst wall is not known. Many of the larger plerocercoids infecting other body cavity sites were also encysted. The relationships between the developmental stage, size, and envelope of these plerocercoids and their migration and infectivity still need to be resolved.

In gonadal tissue of centrarchids, plerocercoid penetration of ovarian expansive stroma, as described by Esch and Huffines (1973), was commonly observed. Penetration of plerocercoids into advanced vitellogenic oocytes, as described by McCormick and Stokes (1982), was rarely observed. The unilateral hypertrophy of infected ovaries in the presence of many plerocercoids was also observed (Figs. 5, 6), with the resulting death of many eggs. Blockage of circulation appeared to have been involved based on the appearance of some blood vessels. Hepatic damage was observed in bluegill by plerocercoids at different developmental stages (Figs. 7, 8). Vacuolation and hepatic necrosis (Fig. 8) were observed on a number of occasions.

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Obituary Notice

RICHARD L. BEAUDOIN

8 June 1931–22 May 1990
Elected Member December 1965
Executive Committee Member-at-Large
1973–1974
Awards Committee 1977, 1982